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SYSTEMATICS OF THE GENUS *HEMITRIAKIS*
(SELACHII: CARCHARHINIDAE), AND
RELATED GENERA

By

L. J. V. Compagno

Division of Systematic Biology, Stanford University

INTRODUCTION

Herre (1923) described *Hemitriakis leucoperiptera*, a new genus and species of shark from the Philippine Islands. *Hemitriakis* was thought to differ from *Triakis* Müller and Henle in its dentition, snout, nasal valves, body, and caudal fin. However, Fowler (1941), Bigelow and Schroeder (1948), Garrick (1954), and Kato (1968) considered *Hemitriakis* a junior synonym of *Triakis*.

Present data shows that *Hemitriakis* is a well defined genus with two species: *H. leucoperiptera* Herre, 1923; and *H. japonica* (Müller and Henle, 1841). This account is a review of the systematics of *Hemitriakis* and related genera in the family Carcharhinidae.

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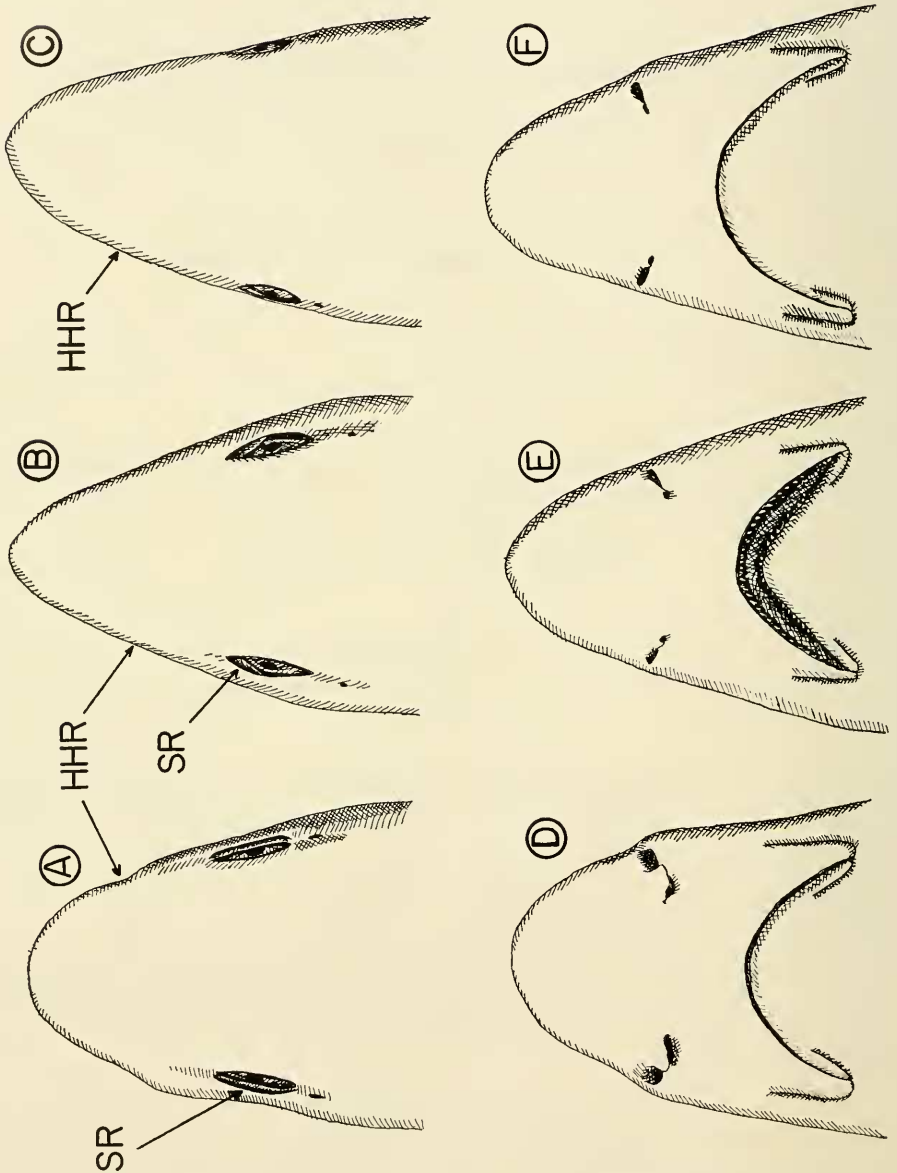


FIGURE 1. A, dorsal view, and D, ventral view, of head of *Hemitriakis japonica* (SU-12677). B, dorsal view of head of *Hypogaleus hyugaensis*, adopted from Miyosi (1939). C, dorsal view, and F, ventral view, of head of *Galeorhinus zyopterus* (LJVC-0238; 847 mm. female.). E, ventral view of head of *Hypogaleus zanzibariensis*, adopted from Smith (1957b). Abbreviations: HHR, horizontal head rim; SR, subocular ridge.

Francisco State College), Robert P. Dempster (Steinhart Aquarium, California Academy of Sciences), and Louis Garibaldi (American Broadcasting Company Marine World, Redwood City, California) supplied many fresh and frozen carcharhinids for anatomical preparations. The late J. L. B. Smith (Department of Ichthyology, Rhodes University, Grahamstown, South Africa) sent specimens of *Eridacnis sinuans* and *Scylliogaleus queckettii*; Leslie W. Knapp (Smithsonian Oceanographic Sorting Center, Washington, D. C.), C. Richard Robins, and Phillip C. Heemstra (Institute of Marine Sciences, University of Miami) loaned other carcharhinids. In addition to providing numerous specimens and research facilities, Shelton P. Applegate (Division of Vertebrate Paleontology, Los Angeles County Museum of Natural History), Susumu Kato (Bureau of Commercial Fisheries Fishery-Oceanography Center, La Jolla, California), and Stewart Springer (Bureau of Commercial Fisheries Systematics Laboratory, U. S. National Museum) have discussed various aspects of carcharhinid taxonomy covered in this paper with me. J. A. F. Garrick (Department of Zoology, Victoria University of Wellington, New Zealand) sent comments on several systematic problems concerning carcharhinid genera and species. George S. Myers critically reviewed the first draft of the manuscript, and Warren C. Freihofer (Division of Systematic Biology, Stanford University) offered useful suggestions. I am most grateful for the help offered by all of these people, without which this account could not have been written.

STUDY MATERIAL

Specimens mentioned in the text and figures are from the collections of the George Vanderbilt Foundation at the California Academy of Sciences (GVF); Division of Systematic Biology, Stanford University (SU); University of Michigan Museum of Zoology (UMMZ); U. S. National Museum (USNM); and of the writer (LJVC).

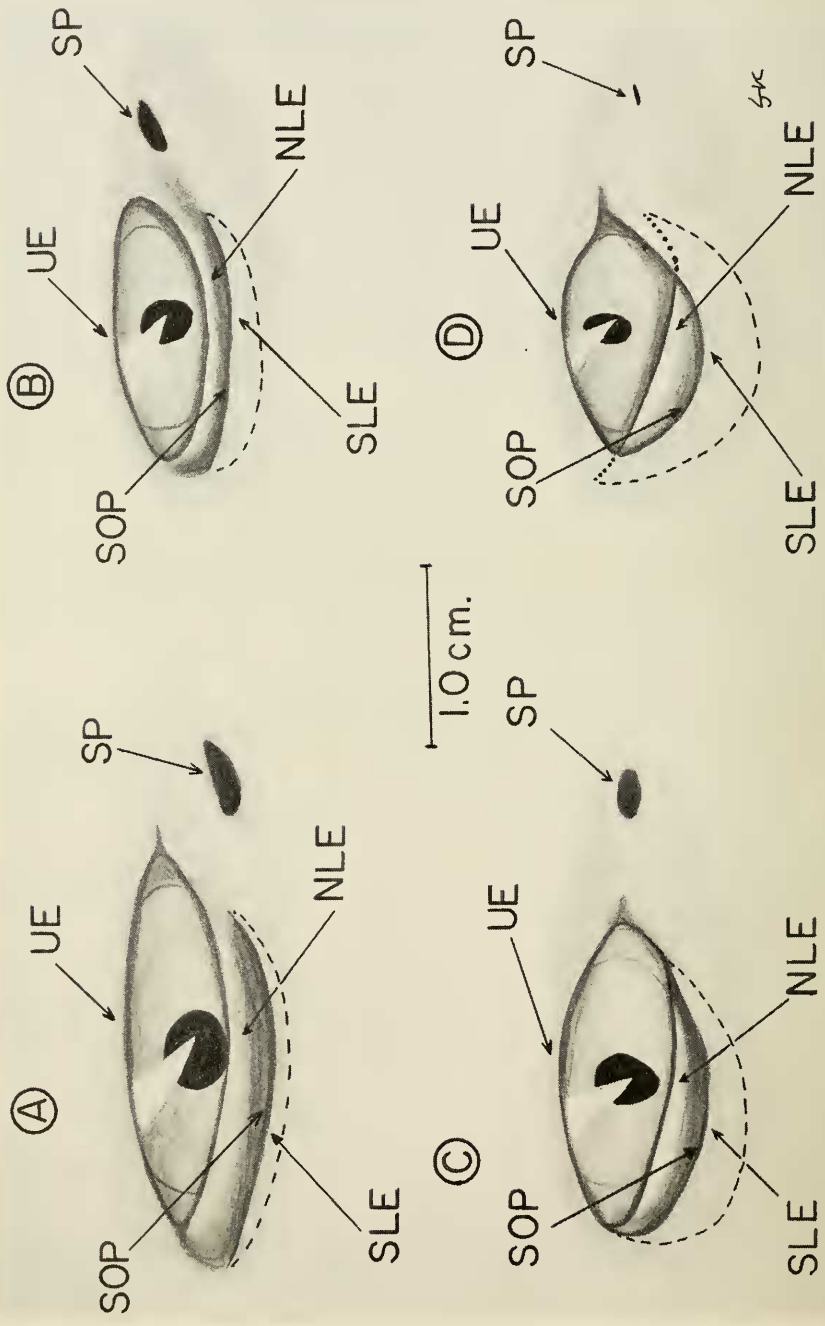
Hemitriakis specimens examined are listed below, with number of specimens and total lengths in parentheses.

Hemitriakis japonica: SU-12677, Nagasaki, Japan (1; 682 mm.); UMMZ-179060, Auraji (Osaki Market, Osaki), Japan (1; 650 mm.); UMMZ-179061, Ainosima (Fukuoka Market, Fukuoka), Japan (1; 560 mm.); UMMZ-179062, Ezumi (Ezumi Market), Japan (1; 505 mm.); USNM-191193, Taipeihsien, Taiwan (3; 651-685 mm.).

Hemitriakis leucoperiptera: SU-27118, Dumaguete, Oriental Negros, Philippine Islands (2; 169-170 mm.).

Hemitriakis species: SU-40097, Dumaguete, Oriental Negros, Philippine Islands (4; 161-180 mm.).

Comparative material including most carcharhinid genera and species was examined. As the number of specimens in this sample is enormous, they are not listed here but will be given in a forthcoming revision of carcharhinid genera.



Instead, the genera and species examined are listed. *Carcharhinus* species nomenclature is modified from Garrick (1967); that for *Scoliodon*, *Rhizoprionodon*, and *Loxodon* is from V. Springer (1964).

Aprionodon isodon, *Carcharhinus acronotus*, *C. albimarginatus*, *C. altimus*, *C. amblyrhynchus*, *C. borneensis*, *C. cauta*, *C. falciiformis*, *C. galapagensis*, *C. leucas*, *C. limbatus*, *C. longimanus*, *C. maculipinnis*, *C. melanopterus*, *C. menisorrhah*, *C. milberti*, *C. obscurus*, *C. pleurotaenia*, *C. porosus*, *C. remotus*, *C. sorrah*, *C. springeri*, *C. tjutjot*, *C. velox*, *Eridacnis barbouri*, *E. radcliffei*, *E. simuans*, *Galeocerdo cuvier*, *Galeorhinus australis*, *G. chilensis*, *G. galus*, "G." *omanensis*, *G. zyopterus*, *Hemigaleus baljouri*, *H. macrostoma*, *H. microstoma*, *H. pectoralis*, *H. tengi*, *Hemipristis elongatus*, *Hypoprion hemiodon*, *H. macloti*, *H. signata*, *Isogomphodon oxyrhynchus*, *Lamiopsis temmincki*, *Leptocharias smithii*, *Loxodon macrorhinus*, *Mustelus antarcticus*, *M. asterias*, *M. californicus*, *M. canis*, *M. dorsalis*, *M. fasciatus*, *M. griseus*, *M. henlei*, *M. hignani*, *M. kanekonis*, *M. lenticulatus*, *M. lunulatus*, *M. manazo*, *M. mento*, *M. mustelus*, *M. norrisi*, *M. schmitti*, *Negaprion acutidens*, *N. brevirostris*, *N. forsteri*, *N. fronto*, *Prionace glauca*, *Proscyllium habereri*, *Rhizoprionodon acutus*, *R. lalandei*, *R. longurio*, *R. oligolinx*, *R. porosus*, *R. terraenovae*, *Scoliodon laticaudus*, *Scylliogaleus quecketti*, *Triaenodon obesus*, *Triakis acutipinna*, "T." *sehlmanni*, *T. maculata*, *T. scyllia*, *T. semifasciata*.

TERMINOLOGY

For descriptive purposes the morphological terminology of the head, eyes, dentition, vertebral column, and fins of carcharhinid sharks is discussed and elaborated here.

HEAD MORPHOLOGY. The horizontal head rim (fig. 1) is the head margin in dorsal or ventral view. The subocular ridge is a ventrolateral expansion of the horizontal head rim beneath the eye. In *Hemitriakis*, *Triakis*, *Mustelus*, *Furgaleus*, and other carcharhinid genera with well developed subocular ridges, the eyes appear medial to the horizontal head rim in dorsal view. A subocular ridge obscures the eyes in ventral view.

NICTITATING LOWER EYELID (fig. 2). Form and terminology of the carcharhinoid ocular structures variously termed nictitating membranes, nictitating

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FIGURE 2. Lateral views of carcharhinid eyes, showing nictitating lower eyelid types. A. *Proscyllium habereri* (UMMZ-179064; 535 mm. female), with rudimentary NLE. B. *Mustelus canis* (USNM-197676; 337 mm. female), with external NLE. C. *Galeorhinus australis* (USNM-176995; 385 mm. male), with transitional NLE. D. *Leptocharias smithii* (USNM-202677; 570 mm. male), with internal NLE. Abbreviations: NLE, nictitating lower eyelid; SLE, secondary lower eyelid; SOP, subocular pouch; SP, spiracle; UE, upper eyelid. Dashed line is bottom of subocular pouch; dotted line in *Leptocharias* is edge of NLE inside palpebral aperture.

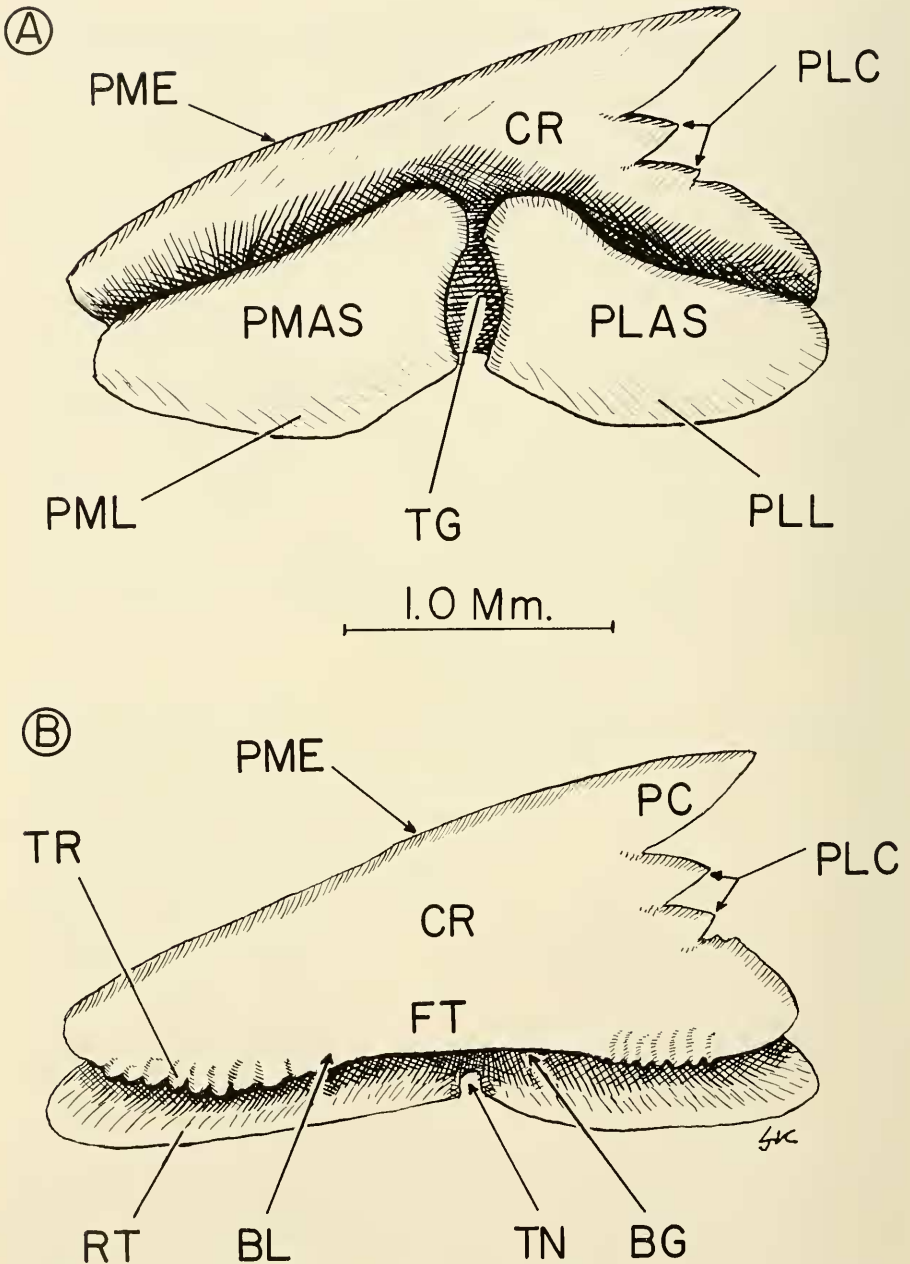


FIGURE 3. Anteroposterior teeth of *Hemitriakis japonica* (SU-12677). A. Inner face of right lower tooth. B. Outer face of left lower tooth. Abbreviations: BG, basal groove; BL, basal ledge; CR, crown; FT, crown foot; PC, primary cusp; PLAS and PMAS,

folds, subocular folds, movable lower eyelids, and nictitans were reviewed by Gilbert (1963) and by Gilbert and Oren (1964). They used the term "nictitans" to cover all variations of the mobile eyelid of scyliorhinids and carcharhinids, but this term is not adopted here as the selachian structure is morphologically and developmentally unlike the true nictitans or nictitating membrane of tetrapods and in many cases is merely a little-modified movable lower eyelid. Instead, the term nictitating lower eyelid (NLE) is introduced to avoid some of the connotations of nictitans and to recognize the probable derivation of the structure from the original lower eyelid of precarcharhinoid sharks.

The exterior fold formed by the groove below the NLE is termed the secondary lower eyelid (SLE). The groove itself is the subocular pouch.

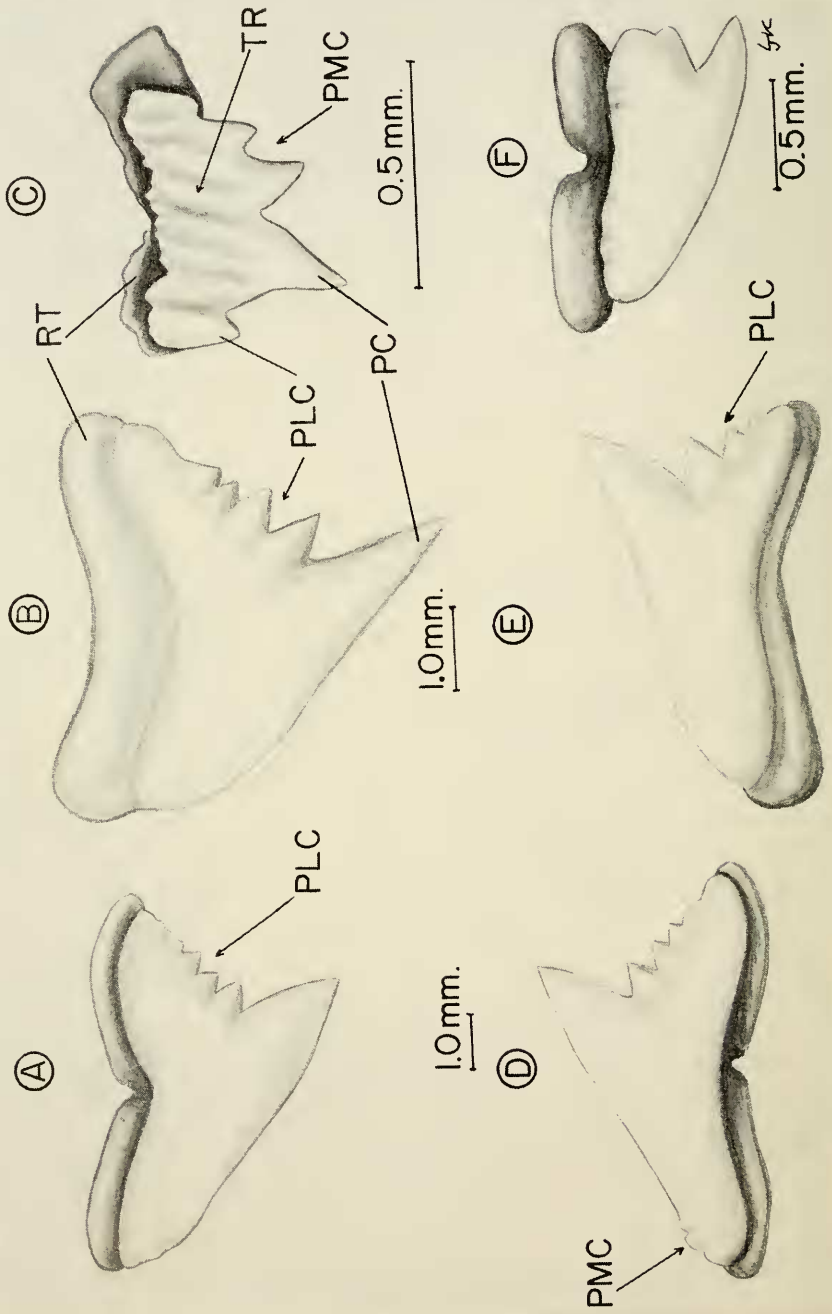
Four nictitating lower eyelid types can be distinguished among carcharhinids if subdivisions are made in the morphological gradient seen in this structure. The rudimentary type is the least specialized. In it the NLE forms the ventral edge of the palpebral aperture and connects anteriorly and posteriorly with the upper eyelid. The SLE is a weak ridge below the NLE and does not connect with either the upper eyelid or the NLE. The upper edge of the SLE is not defined and the subocular pouch is a very shallow, external groove. The external type differs from the rudimentary in that the SLE is a strong flap with a well defined edge. The subocular pouch, although relatively shallow, is strongly differentiated. The internal type is the most advanced, with the NLE ends entirely internal to the palpebral aperture and not connected to the upper eyelid. The SLE replaces the NLE in contacting the anterior and posterior ends of the upper eyelid and forms the ventral edge of the palpebral aperture. The subocular pouch is entirely within the palpebral aperture and varies from moderately shallow (*Leptocharias*) to very deep (*Carcharhinus*). The transitional type covers intermediates between internal and external types. These often have the SLE attached by one of its ends (posterior or anterior) to the upper eyelid, while the NLE has its opposite end also attached to the upper eyelid.

DENTITION (figs. 3-4). Tooth topography of selachians was discussed briefly by Applegate (1967). He divides the tooth into two external regions, the crown and the root. The crown is the enamel-covered region of the tooth distal to its attachment with the jaw. The proximal root lacks the enamel covering and has its component osteodentine exposed to the surface. The region of the crown proximal to the root is termed the foot. As used by Bigelow and Schroeder (1948), the term base includes both the root and the crown foot.

The crown and root are both compressed in a plane with its horizontal sides

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postlateral and premedial parts of attachment surface; PLC, postlateral cusplets; PLL, postlateral lobe of root; PME, premedial edge of crown; PML, premedial lobe of root; RT, root; TG, transverse groove; TN, transverse notch; TR, transverse ridges.



parallel to the jaw axis and its vertical sides perpendicular to it. Teeth in upright functional positions at the edge of the jaw have outer and inner faces on their planes of compression. The orientations of these faces are reversed when the teeth are in replacement position but as a convention the functional orientation is used here for any tooth.

The root has its inner face partially formed into a flattened attachment surface that seats in the dental membrane against the jaw surface. The root has a vertical transverse groove that superficially divides the attachment surface into two lobes and may extend over the extreme rim of the root to form a transverse notch. The outer face of the root may have a strong basal groove extending horizontally across it that is overlapped by a strong basal ledge of the crown foot. A series of vertical transverse ridges may be present on the basal ledge and often extend distally on the outer face of the crown. In many species of *Mustelus* the crown inner face has a rounded protuberance or peg. The peg of one tooth extends into the basal groove of the next tooth in succession in the same row, an arrangement that may serve to interlock the teeth in the pavement dentitions of these forms.

The distal part of the crown, as opposed to the foot, may have its margin in the plane of its compression formed into a sharp cutting edge, with or without serrations. Pointed projections from the crown edge are termed cusps or cusplets according to their size relative to each other. In carcharhinids a median primary cusp is commonly present and is usually larger than other projections of the crown edge (when such are present). The primary cusp may have its axis perpendicular or oblique to the tooth base. Its proximal origin may occupy all or only part of the foot. When a primary cusp origin is restricted, the adjacent crown edges may be formed into other cusps or cusplets, sharp-edged blades, or rounded shoulders.

The planes of compression in the teeth of carcharhinid sharks have their horizontal sides parallel to the jaw axis, but this axis changes from nearly perpendicular to the body axis at the symphysis to nearly parallel with the body axis at either end of the dental arcade. The horizontal sides of the planes of compression for tooth roots and crowns are therefore oriented in an anteromedial-to-posterolateral direction relative to the anterior-to-posterior horizontal body axis along

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FIGURE 4. Outer views of carcharhinid teeth. All teeth except C from left half of dental band. A, upper 8th tooth, and D, lower 10th tooth, of *Galeorhinus zyopterus* (LJVC-0114; 1670 mm. male). B, upper 10th tooth, and E, lower 9th tooth, of *Hypogaleus zanzibariensis* (1220 mm. male; modified from Smith, 1957b). C. Upper tooth of third row from end of dental band, *Proscyllium habereri* (GVF-Hong Kong-88; 523 mm. female). F. Same of *Triakis semifasciata* (LJVC-0137; 1097 mm. male). Abbreviations as in Figure 3, except for: PMC, premedial cusplets.

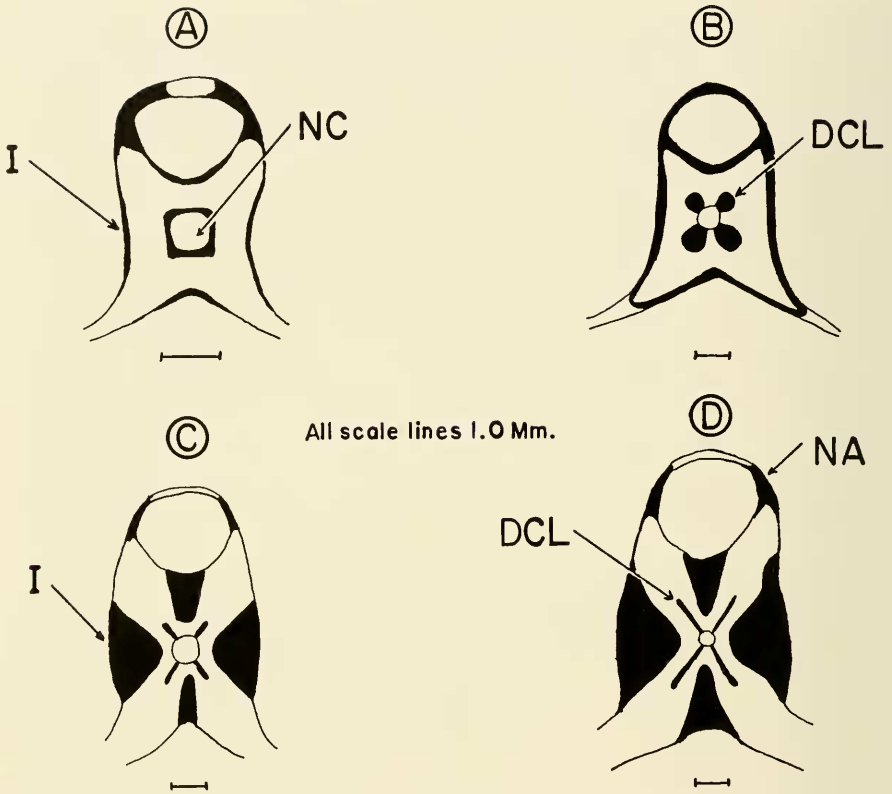


FIGURE 5. Transverse views of carcharhinid vertebral calcification patterns, with calcified areas indicated in black. A. *Eridacnis barbouri* ("Silver Bay" 3514; 258 mm. female). B. *Proscyllium habereri* (UMMZ-179065; 565 mm. male). C. *Mustelus henlei* (LJVC-0020; 630 mm. female). D. *Hemitriakis japonica* (SU-12667). Abbreviations: DCL, diagonal calcified lamellae; I, intermedialia; NA, neural arch; NC, notochordal canal.

most of the jaw, with the angle between the sides and the body axis decreasing from symphysis to rictus. It is possible with these orientations to distinguish anteromedial and posterolateral edges on the crowns and anteromedial and posterolateral lobes on the roots of most teeth. Exceptions occur at the symphysis, where teeth may have medial-to-lateral orientation, and at the ends of the dental arcade, where teeth can have anterior-to-posterior orientation. As a convention the anteromedial-to-posterolateral relations are used for all teeth. For brevity, structures having an anteromedial orientation on the tooth are termed premedial, whereas posterolateral structures are postlateral. Thus, carcharhinid teeth can have premedial and postlateral cusp edges, cusplets, serrations, blades, etc.

The terms row and series were used almost interchangeably by Bigelow and

Schroeder (1948), but Applegate's (1965) usage is followed here. A row is a single replicating file of teeth approximately transverse to the jaw axis that includes both functional teeth and their replacements in various stages of development. The row represents an entire family of teeth derived from one germinal area on the jaw. The term "series" is used for a line of teeth along the jaws which is parallel to the jaw axis and includes teeth from all rows present. In some carcharhinids, especially those with pavement dentitions and very numerous teeth, the concept of series may be meaningless as all teeth are closely adpressed in quincunx formation and do not form distinct transverse lines.

As indicated by Applegate (1965), there are two primary types of heterodonty, or differentiation between teeth in various positions on the jaws, that can be demonstrated in sharks. The first, here termed dignathic heterodonty, involves differences in morphology between teeth in opposition or approximate opposition in the upper and lower jaws. Dignathic heterodonty can apply to all opposing teeth in both jaws or to only some of them. The second type, monognathic heterodonty, involves differences between teeth in different positions on the same jaw series. Monognathic heterodonty is not restricted to situations in which adjacent teeth differ strongly in morphology, but also applies when a tooth in one position is different from that in another position on the same series but has a gradient of intermediate teeth between itself and the second tooth. The first condition can be called disjunct monognathic heterodonty; the second, gradient monognathic heterodonty.

Applegate (1965) used a row-group terminology for implied disjunct monognathic heterodonty in the dentitions of *Odontaspis taurus* (Odontaspidae) and other sharks. The terms symphysials, alternates, and medials were used for different tooth types in the region of the symphysis. Remaining teeth were grouped into anteriors, intermediates, laterals, and posteriors from premedial to postlateral along the dental band. Analogs of the intermediates in lamnoids do not exist in carcharhinids. However, some carcharhinid genera, especially those in the advanced and intermediate groupings mentioned below, show strong disjunct monognathic heterodonty and have medials, alternates, symphysials, anteriors, laterals, and posteriors. Other genera (as *Hemitriakis*) have disjunct variation only between the medials or alternates at the symphysis and the adjacent parasymphysial rows, which may be termed anteroposteriors.

Two additional types of heterodonty can be defined here. Ontogenic heterodonty is a gradient phenomenon in which tooth morphology at a functional series position in a single row or many rows changes with replacement of teeth during growth. Gynandric heterodonty, or dental sexual dimorphism, includes differences in morphology of teeth in approximately similar series and row positions between two individuals or groups of individuals of opposite sex and same species at about the same developmental stage.

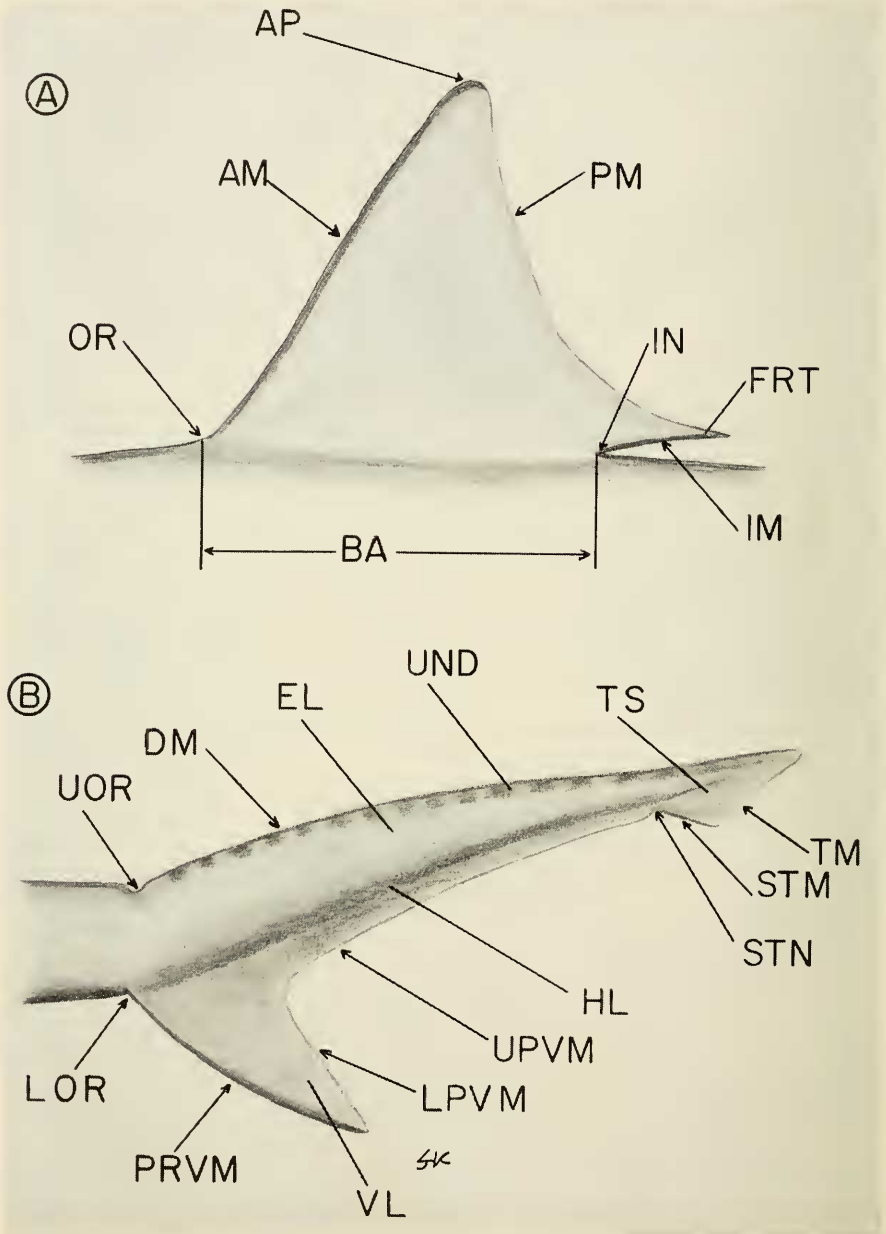


FIGURE 6. Carcharhinid fin terminology. A. Idealized first dorsal fin. B. Caudal fin. Abbreviations: AM, anterior margin; AP, apex; BA, base; DM, dorsal margin; EL, epural lobe; FRT, free rear tip; HL, hypural lobe; IM, inner margin; IN, insertion; LOR, lower origin; LPVM, lower postventral margin; OR, origin; PM, posterior margin;

VERTEBRAE. Terminology for vertebral calcified parts follows Ridewood (1921).

Springer and Garrick (1964) subdivided the vertebral complements of sharks into precaudal and caudal centra. They noted that an alternative grouping into monospondylic and diplospondylic centra was possible, but this was not utilized in their study.

For present purposes the Springer and Garrick dichotomy of vertebral types is modified into a three-group system of monospondylic precaudal (MP), diplospondylic precaudal (DP), and diplospondylic caudal (DC) centra. This trichotomy is applicable to most carcharhinids, but breaks down in sharks such as *Galeorhinus zyopterus* where alternating long and short centra of a "stutter zone" mark the transition from MP to DP centra. Springer and Garrick's method of delimiting the caudal centra at the upper precaudal pit or upper caudal origin is followed here despite its shortcomings.

In some instances it is useful to compare relative numbers of centra in different vertebral groups of sharks with differing total vertebral counts. A system used here divides the MP, DP, and DC counts by the MP count to give DP/MP and DC/MP ratios that vary sufficiently between carcharhinid genera and species to be of systematic value (MP/MP = 1.00). An alternate system is to divide MP, DP, and DC counts by total count and multiply by 100 to obtain percent total count for each vertebral group.

FINS. The terminology used here for carcharhinid fins is explained by fig. 6. The following terms apply to paired and unpaired fins other than the caudal: Origin; anterior margin; apex; posterior margin; free rear tip; inner margin; insertion; and base. The caudal fin terminology includes: Hypural lobe; epural lobe; terminal sector; subterminal notch; ventral lobe; dorsal margin; terminal margin; subterminal margin; upper postventral margin; lower postventral margin; preventral margin; upper origin; and lower origin.

Genus *Hemitriakis* Herre, 1923

TYPE SPECIES. *Hemitriakis leucoperiptera* Herre, 1923, by original designation.

SPECIES. There are two named species: *H. leucoperiptera*, from the Philippine Islands (detailed distribution in Herre, 1953); and *H. japonica* (Müller and Henle), from Japan, Taiwan, and Amoy (Chen, 1963).

Hemitriakis japonica was placed in the genus *Galeorhinus* Blainville (or its junior synonyms, *Galeus* Cuvier, 1817, not Rafinesque, 1810, and *Eugaleus* Gill)

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PRVM, preventral margin; STM, subterminal margin; STN, subterminal notch; TM, terminal margin; TS, terminal sector; UND, undulations in dorsal caudal margin; UOR, upper origin; UPVM, upper postventral margin; VL, ventral lobe.

by all previous writers (summarized in Fowler, 1941, and Chen, 1963). The species was named *Galeus japonicus* by Müller and Henle (1841).

Specimens of *Galeorhinus japonicus* were compared with specimens of *Galeorhinus australis*, *G. chilensis*, *G. galeus* (type species of *Galeorhinus*), *G. zyopterus*, and with specimens and Herre's (1923) description of *Hemitriakis leucoperiptera*. This indicated that "*japonicus*" does not belong to *Galeorhinus* but is congeneric with *Hemitriakis leucoperiptera*.

The two *Hemitriakis* species are close but *H. leucoperiptera* differs from *H. japonica* in having the first dorsal origin over inner pectoral margin (*H. japonica* with origin posterior to free rear tip of pectoral). The distance from pectoral free rear tips to pelvic origins about equal to first dorsal length from origin to free rear tip in *H. leucoperiptera* but much greater in *H. japonica*. *Hemitriakis leucoperiptera* also has fewer vertebrae, with about 144–146 total count (2 specimens) and 34–35 MP centra (*H. japonica* with 156–161 total and 41–43 MP centra for 7 specimens).

An undescribed *Hemitriakis* species may be represented by 4 specimens (SU-40097) that differ from the sympatric *H. leucoperiptera* in various proportions, fin shapes, and in their strikingly barred and spotted coloration (*H. leucoperiptera* and *H. japonica* have a nearly plain coloration).

REDEFINITION AND DESCRIPTION OF THE GENUS *Hemitriakis*. Head flattened dorsoventrally, its length from snout tip to 5th gill opening about $\frac{1}{3}$ of total length. Eyes high on sides of head, above horizontal head rim and level of nostrils by a space equal or greater than eye height (fig. 7A). Strong subocular ridge present, in dorsal view separating eyes from horizontal head rim by a wide space (fig. 1A). Eyes not visible in ventral view of head (fig. 1D). Eyes elongate, their apertures over twice as long as high, with a notch present posteriorly in adults and subadults. NLE external (fig. 7A), with its edge horizontal. Edge of SLE strongly differentiated. Subocular pouch shallow but well defined, with its interior surface covered with denticles.

Spiracles present, slitlike or porelike, $1\frac{1}{5}$ to $1\frac{1}{7}$ of eye length. External gill openings short, the longest (3rd) less than eye length. Gill rakers absent from internal gill openings.

Nostrils narrow, far apart, a nostril width about $2\frac{1}{2}$ times in internarial width. Anterior nasal flap a short rounded lobe, not a pointed barbel. Nostrils about half as far from mouth as from snout tip. Nasoral grooves absent.

Mouth crescentic, broad, at least $2\frac{1}{3}$ times as wide as long. Large papillae absent from buccal cavity. Moderately long labial furrows present, upper about $1\frac{1}{2}$ times as long as nostril width, the lower $\frac{1}{3}$ to $\frac{2}{3}$ of upper. Upper labial furrows extending anteriorly to below first $\frac{1}{4}$ of eye.

Dignathic heterodonty weak, with upper anteroposterior teeth slightly larger and with higher crowns and more erect cusps than lowers; upper medials smaller

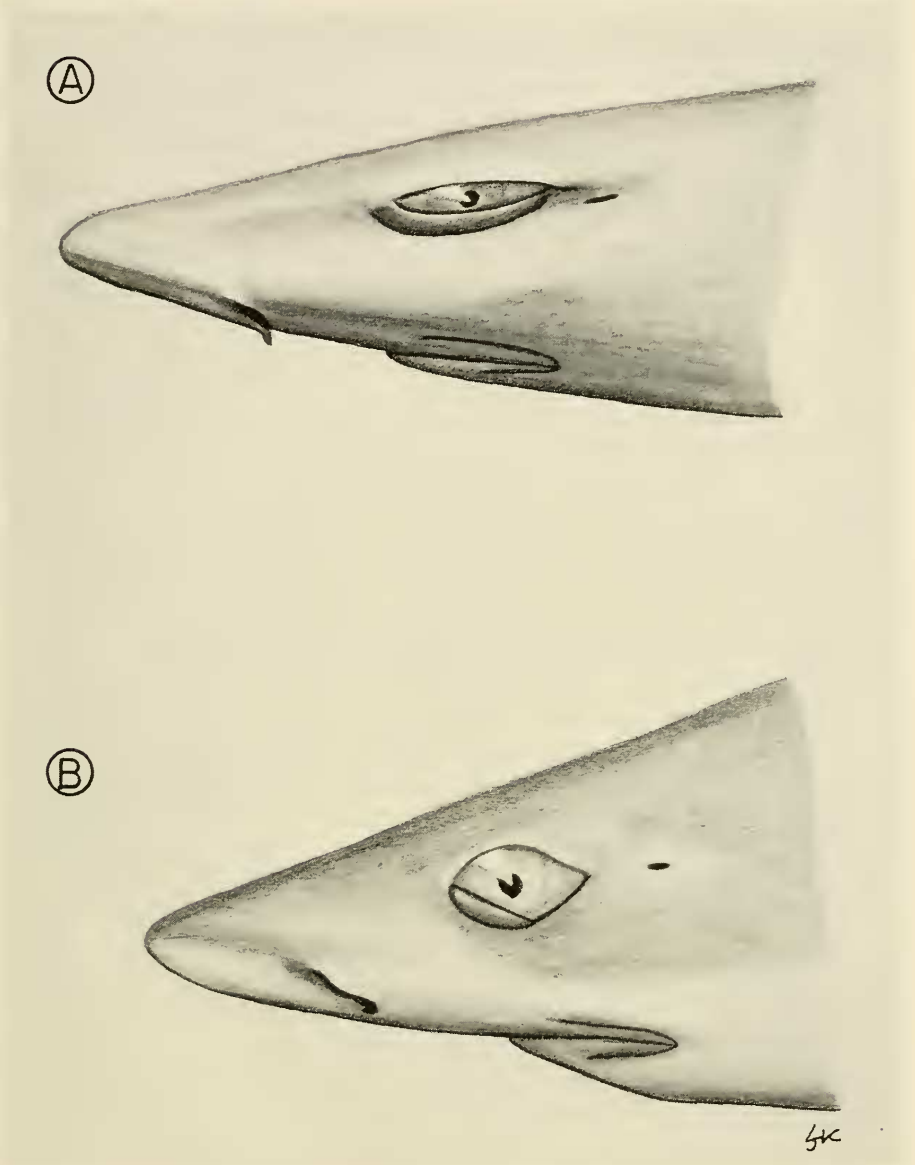


FIGURE 7. Lateral view of carcharhinid heads. A. *Hemitriakis japonica* (SU-12677). B. *Galeorhinus zyopterus* (LJVC-0238).

than lower ones. Disjunct monognathic heterodonty indicated by differentiation of 3 to 6 rows of medials in upper and lower jaws. Medial teeth differ from anteroposteriors in their lesser size and erect primary cusps, flanked by 1 or 2

premedial and postlateral cusplets. The sharp-edged anteroposteriors are larger, compressed, bladelike cutting teeth with a strong oblique primary cusp and no premedial cusplets (fig. 3). Anteroposteriors show strong gradient monognathic heterodonty. In more premedial teeth in adults and subadults the primary cusp is large and has 2 to 4 postlateral cusplets flanking it. From premedial to postlateral the crowns of teeth become lower, the primary cusps become more oblique, and the postlateral cusplets become fewer and finally disappear. The most postlateral anteroposteriors have primary cusps reduced or absent and are very low and sharp-keeled. Ontogenic heterodonty present in more premedial teeth of anteroposteriors. These teeth gain more postlateral cusplets with growth, so that late embryos have no cusplets and adults have 2 to 4 cusplets. Gynandric heterodonty not apparent.

Teeth moderately large, base width of longest lower anteroposteriors about 0.356–0.405 percent of total length in *H. japonica*. Tooth rows relatively few; Chen (1963) gives 23–29/27–33 (4 specimens) and Tang (1934) gives 35/33 (1 adult male) total tooth row counts for *H. japonica*. The 7 examples of *H. japonica* studied here have 33–38/29–33 rows. Herre (1923) gives 18/34 rows for the holotype (adult female) of *H. leucoperiptera*, but this may be erroneous as 33/30 rows were counted in one of the SU–27118 specimens (late embryo). One to 5 series functional along jaw edges. Teeth of adjacent rows in the alternate overlap pattern of Strasburg (1963). Serrations absent from crown edges. Crown premedial edge not indented and differentiated. Crown foot with a strong basal ledge overlapping a deep basal groove. Transverse ridges present on basal ledge only, not extending onto primary cusp. Roots low, deep, with strong transverse groove dividing attachment surface into 2 lobes and extending through extreme rim of root to form strong transverse notch. Teeth not noticeably protruding when mouth is closed.

Trunk not compressed, subcylindrical. Interdorsal ridge present. Lateral dermal keels absent from caudal peduncle. No precaudal pits. Head-trunk length from snout tip to cloaca equal to, or somewhat shorter than, tail length from cloaca to caudal tip.

Denticles from sides of body below first dorsal fin small, with crowns much longer than wide at all sizes. A single strong medial cusp and bifurcated longitudinal ridge with a weak lateral ridge on each side of crowns of adult denticles. In late embryos to subadults medial ridge not bifurcated and lateral ridges absent. A pair of weak lateral cusps often present on denticles, but these are not constant.

Pectorals moderately large, pectoral area slightly greater than first dorsal area. Pectoral anterior margin about $1\frac{1}{2}$ times as long as combined base and inner margin lengths. Apex of adpressed pectoral slightly posterior to its free rear tip when pectoral inner margin is held parallel to body axis. Origin of

pectoral below or slightly anterior to fourth gill opening. Pectoral skeleton projecting about $\frac{2}{3}$ to $\frac{1}{2}$ of pectoral anterior margin length into the fin. Distal pectoral radials slightly longer than proximal ones, with broad, truncate tips.

Pelvic relatively small, their anterior margins less than $\frac{1}{2}$ the length of pectoral anterior margins. Pelvic bases closer to 1st dorsal base than to 2nd dorsal base.

Midpoint of 1st dorsal base almost equidistant between pelvic and pectoral bases or definitely closer to pectoral bases. First dorsal free rear tip anterior to pelvic origins.

Second dorsal nearly as large as first one, with its height 70 to 80 percent of 1st dorsal height. Posterior margin of 2nd dorsal strongly concave.

Anal much smaller than 2nd dorsal, its height $\frac{1}{2}$ that of 2nd dorsal and its base only $\frac{2}{3}$ to $\frac{3}{4}$ of 2nd dorsal base. Anal posterior margin strongly concave in adults, shallowly concave in late embryos. Anal origin posterior to 2nd dorsal origin by about $\frac{1}{3}$ of the 2nd dorsal base length. Anal insertion varying from under 2nd dorsal insertion to much less than $\frac{1}{3}$ of 2nd dorsal base length posterior to it.

Caudal with preventral and postventral margins expanded as a short ventral lobe in adults and subadults, but scarcely developed in late embryos. Preventral caudal margin over $\frac{1}{3}$ of dorsal caudal margin in adults and subadults, slightly shorter in young. Postventral margin differentiated into upper and lower parts in subadults and adults, with upper postventral margin $\frac{1}{3}$ to $\frac{2}{3}$ of dorsal caudal margin. Subterminal caudal margin long, over $\frac{1}{2}$ of terminal caudal margin length. Caudal short, dorsal margin about equal to head length and less than $\frac{1}{4}$ of total length. No lateral undulations in dorsal caudal margin. Terminal sector of caudal short; distance from subterminal notch to caudal tip only about $2\frac{1}{2}$ to 3 times in dorsal caudal margin. Vertebral axis of caudal slightly raised above body axis.

Vertebrae moderately numerous, total count 144–161. Separation between MP and DP centra not sharp, gradual along two transitional centra. Vertebral calcification pattern of Applegate's (1967) "carcharhinoid" type.

Chondrocranium very similar to that of *Furgaleus ventralis* as illustrated by Whitley (1948) and to that of *Mustelus* species described and illustrated by Gegenbaur (1872) and Holmgren (1941). Supraorbital crest of cranium strongly developed and entire.

Intestinal valve of spiral type, with 6 to 8 turns in the spiral.

Hemitriakis is livebearing and probably viviparous. Yolk-sac placentae are present on the SU-40097 (late embryo) specimens.

FAMILIAL CLASSIFICATION OF *HEMITRIAKIS*

The familial classification of the genus *Hemitriakis* is troublesome because one of its species, *H. japonica*, is conventionally placed in the family Carcharhin-

idae as delimited by Bigelow and Schroeder (1948). In contrast, *H. leucoperiptera* is usually placed in the family Triakidae. *Hemitriakis* cannot simultaneously reside in both families, but the problem goes beyond deciding in which family this genus belongs. This is because *Hemitriakis* is almost exactly intermediate between the Triakidae and Carcharhinidae as defined by modern writers. Hence the selection of a family for *Hemitriakis* is dependent on the validity of separating the Triakidae from the Carcharhinidae.

According to Bigelow and Schroeder (1948) and to Garrick and Schultz (1963), triakids differ from carcharhinids only by NLE morphology and dentition. The triakids are supposed to have rudimentary, external, and transitional NLE types (except for *Leptocharias* and *Triacnodon* with an internal NLE), whereas carcharhinids have an internal NLE. The teeth of triakids are small, crushing molariform or bladelike multicuspidate types that are present in several functional series on the jaw sides. Carcharhinid teeth are small to large, blade-like, with not more than 1 or 2 series of teeth functional at the sides of the jaws.

As noted by Garrick and Schultz, the separation of the two families is confounded by the seemingly intermediate positions of *Triacnodon*, *Leptocharias*, and *Hemitriakis japonica*. *Triacnodon* especially strains the classification by having "triakid" teeth and an internal NLE. However, Gohar and Mazhar (1964) claimed that *Triacnodon* belonged in the Carcharhinidae because it has a scroll intestinal valve as in *Carcharhinus* and other advanced genera. An unpublished study of the morphology of *Triacnodon obesus* confirms Gohar and Mazhar's results on the valvular intestine and also demonstrates that *Triacnodon* is very different from other "triakids" in its cranial morphology, pectoral fin skeletal structure, head morphology, and many other characters. Of the various triakid and carcharhinid genera, *Negaprion* is evidently closest to *Triacnodon*. The teeth of *Triacnodon* superficially resemble those of other "triakids" only in having premedial and postlateral cusplets flanking a primary cusp, but are otherwise strikingly different in the advanced morphology of their crowns and roots. It is probable that the "triakid" characters of *Triacnodon* are convergent ones.

Even without *Triacnodon* to complicate the issue, the familial separation of Triakidae from Carcharhinidae, using the traditional characters, fails when other genera are considered. Thus, *Hemitriakis* had bladelike, sharp-edged anteroposterior teeth in 1 to 5 functional series that closely resemble those of *Galeorhinus*, but has medials with multiple premedial and postlateral cusplets closely resembling "triakid" teeth. Its NLE is external, as in many, but not all, supposed triakids. *Furgaleus* combines *Galeorhinus*-like upper anteroposterior teeth, *Hemigaleus*-like lower anteroposteriors with one erect primary cusp and no cusplets, and an external NLE. *Furgaleus* is conventionally placed in the Triakidae. Another triakid, *Leptocharias*, has an internal NLE and

anterolateral teeth with primary cusps, premedial cusplets, and postlateral cusplets in the "triakid" pattern. In the genus *Galcorhinus* (a presumed carcharhinid), young specimens of *G. australis*, *G. chilensis*, *G. galeus*, and *G. zyopterus* have a transitional NLE, but half-grown to adult individuals have these structures internal. Finally, *Triakis semifasciata* and *T. scyllia* have an external NLE in young specimens but this changes to a transitional or fully internal one in adults and subadults. Adult and subadult *Mustelus* commonly have a transitional NLE, but large *M. canis* may have the internal type (Garman, 1913; Bigelow and Schroeder, 1948). The teeth of *Triakis semifasciata* are arranged in only 3-4 functional series on the jaw edge. Also, in *T. semifasciata* the teeth show considerable ontogenic heterodonty, with loss of premedial and postlateral cusplets as the dentition is replaced until many to almost all of the teeth in adult specimens have only a strong, oblique primary cusp. *Triakis maculata* also shows a similar type of ontogenic heterodonty (Kato, Springer, and Wagner, 1967).

The orthodox distinction of Triakidae from Carcharhinidae is untenable at present because the supposedly diagnostic and traditional characters used to separate these families fail to do so. As the above examples show, there are enough transitional genera and species to make the retention of the two families Triakidae and Carcharhinidae an arbitrary choice based on tradition and convenience. I prefer to submerge the Triakidae in the Carcharhinidae. This has the obvious disadvantage of creating a huge, unwieldy, and heterogeneous complex that combines advanced forms with scyliorhinoid genera. However, it may be possible eventually to divide the family Carcharhinidae as here constituted into a number of lesser families using new characters of comparative morphology that are now being investigated.

Hence, the genus *Hemitriakis* is considered a member of the expanded family Carcharhinidae.

COMPARISON WITH OTHER GENERA

This section demonstrates the distinctness of *Hemitriakis* from other carcharhinid genera. A series of synoptic keys is presented in which allied groups of genera are compared and contrasted with *Hemitriakis*. A general key to carcharhinid genera is not offered here as revisional studies on the family are incomplete at present.

To facilitate comparison of *Hemitriakis* with certain genera, it was necessary to include some species rearrangements within them in the following discussions. This primarily involved removal of some species from the heterogeneous genera *Triakis* and *Galcorhinus* and proposal of tentative new generic arrangements to accommodate them.

ADVANCED AND INTERMEDIATE CARCHARHINIDS. A large proportion of car-

charhinid genera comprise the two groups here termed the advanced and intermediate carcharhinids. The advanced genera include *Aprionodon*, *Carcharhinus*, *Galeocerdo*, *Hypoprion*, *Isogomphodon*, *Lamiopsis*, *Loxodon*, *Negaprion*, *Prionace*, *Rhizoprionodon*, *Scoliodon*, and *Triaenodon*. The intermediate genera are *Hemigaleus* (including *Chaenogaleus*, *Negogaleus*, and *Paragaleus*) and *Hemipristis* (including *Dirrhizodon* and *Heterogaleus*).

The advanced carcharhinids are so named because they depart furthest of all genera in the family from the morphology of generalized scyliorhinid genera widely thought to occupy the most primitive position among carcharhinoid sharks. The Sphyrnidae (hammerheads) is closely allied to the advanced carcharhinids but is not included for comparison with *Hemitriakis* because of its unique and obvious specializations. The intermediate genera are very similar to the advanced ones in many characters, but retain some generalized features in the morphology of the cranium, fins, dentition, and intestinal valve.

The advanced and intermediate carcharhinids are grouped together for brevity to compare them with *Hemitriakis*. The following synopsis covers only a representative sample of numerous differences between these genera and *Hemitriakis*.

1a. Eyes low on head, their ventral margins meeting or extending across the horizontal head rim. Subocular ridge weak or obsolete. NLE always internal, with slanted edge. Subocular pouch very deep, with inner surface of SLE and bottom of pouch lacking denticles. Crowns of teeth without a strong basal ledge and groove (except in lower teeth of *Hemigaleus*). Transverse ridges virtually absent from crown foot. Denticles of adults as wide or wider than long, with three or more subequal cusps and ridges. Precaudal pits present always at upper caudal origin and usually at lower origin also. Pectoral skeleton projecting at least $\frac{2}{3}$ of pectoral anterior margin length into fin, with distal radials much longer than proximals. Distal radials with tapering, acute tips. Anal large relative to 2nd dorsal, its height 70 per cent or more of 2nd dorsal height. Lateral undulations present along dorsal caudal margin (except in young of some species and in *Scoliodon* where undulations are indifferently developed). Intestinal valve a scroll in advanced carcharhinids, but a spiral with only 2-6 turns in *Hemigaleus* and *Hemipristis*. Chondrocranium with isolated preorbital and postorbital processes only, without an intermediate supraorbital crest . . . Advanced and Intermediate Carcharhinids.

1b. Eyes high on head, their ventral margins widely separated from the horizontal head rim in ventral view. Subocular ridge very strong. NLE external, with edge horizontal. Subocular pouch shallow, with denticles covering its internal surface. Crowns of teeth with strong basal groove and ledge. Transverse ridges irregularly present on crown foot. Denticles of adults longer than wide, with a very strong medial ridge and cusp and flanking weak lateral ridges also; weak lateral cusps irregularly present. Precaudal pits absent. Pectoral fin skeleton projecting only $\frac{2}{3}$ to $\frac{1}{2}$ of pectoral anterior margin distance into fin, with distal radials slightly longer than proximals. Distal radials with parallel articulating edges and truncate tips. Anal relatively small in relation to second dorsal, its height only $\frac{1}{2}$ that of second dorsal height. Lateral undulations of dorsal caudal margin absent. Intestinal valve a spiral, with 6-8 turns. Chondrocranium with strong supraorbital crest between preorbital and postorbital processes *Hemitriakis*.

GALEORHINUS AND ALLIED GENERA. Recent workers have included the following species in *Galeorhinus*: *G. galeus* (Linnaeus, 1758); *G. japonicus* (Müller and Henle, 1841); *G. australis* (Macleay, 1881); *G. zyopterus* (Jordan and Gilbert, 1883); *G. chilensis* (Perez Canto, 1886), including *G. molinae* (Philippi, 1887); *G. omanensis* (Norman, 1939); *G. hyugaensis* Miyosi, 1939; *G. vitaminicus* de Buen, 1950; and *G. zanzibariensis* Smith, 1957. Of these nine species, four are sufficiently different to require removal from *Galeorhinus*. "*Galeorhinus*" *japonicus* has been already transferred to *Hemitriakis*. *G. hyugaensis* and the closely similar *G. zanzibariensis* are placed in the genus *Hypogaleus* and discussed below. "*Galeorhinus*" *omanensis*, as suggested by its describer (Norman, 1939), is not congeneric with *Galeorhinus* and will be discussed in a forthcoming paper by Mr. Stewart Springer and myself. It is included in the synopsis below to distinguish it from *Hemitriakis*.

The remaining 5 nominal species comprise the genus *Galeorhinus* as here delimited. Garman (1913), Fowler (1929, 1941), and Bigelow and Schroeder (1948) considered *G. zyopterus* a junior synonym of *G. galeus*, while Kato, Springer, and Wagner (1967) tentatively synonymized *G. chilensis* with *G. zyopterus*. McCoy (1885) compared *G. australis* with *G. galeus* and listed several proportional differences between a few specimens of *G. australis* and one of *G. galeus*. However, comparison of a pair of equal sized specimens of *G. galeus* and *G. australis* suggests that most, if not all, of McCoy's differences were allometric ones based on comparison of dissimilar sized specimens. *G. vitaminicus*, as described by De Buen (1950), is hardly different from other *Galeorhinus* species. It may be that all 5 species are synonyms, as Smith (1957b) maintained, but the validity of this hypothesis cannot be tested at present because of insufficient material.

Smith (1957b) proposed the subgenus *Hypogaleus* for its type, *Galeorhinus* (*Hypogaleus*) *zanzibariensis* Smith, 1957, and for *Hemitriakis japonica*. According to Smith, *Hypogaleus* species have teeth without the transverse notch on their roots, but in *Galeorhinus* (including only *G. galeus*) the notch is present. In *Galeorhinus* the caudal terminal sector is large, about $\frac{1}{2}$ caudal length, but much smaller and less than $\frac{1}{2}$ caudal length in *Hypogaleus*. *Hypogaleus* has the second dorsal at least twice as great in area as anal, but *Galeorhinus* has these fins subequal in size. In *Galeorhinus* the pelvic fins of adults are inserted behind the middle of the total length; in *Hypogaleus* the pelvics of adults are inserted well in advance of the middle of the total length.

Apparently Smith used only literature descriptions for *Hemitriakis japonica*. Although most of the fin characters for *Hypogaleus* fit *Hemitriakis japonica*, the dentitional character does not, as this species has a strongly developed transverse notch. Also, Smith's tooth photographs of *G. (Hypogaleus) zanzibariensis* seem to indicate that this species has much higher roots and obsolete basal ledges and

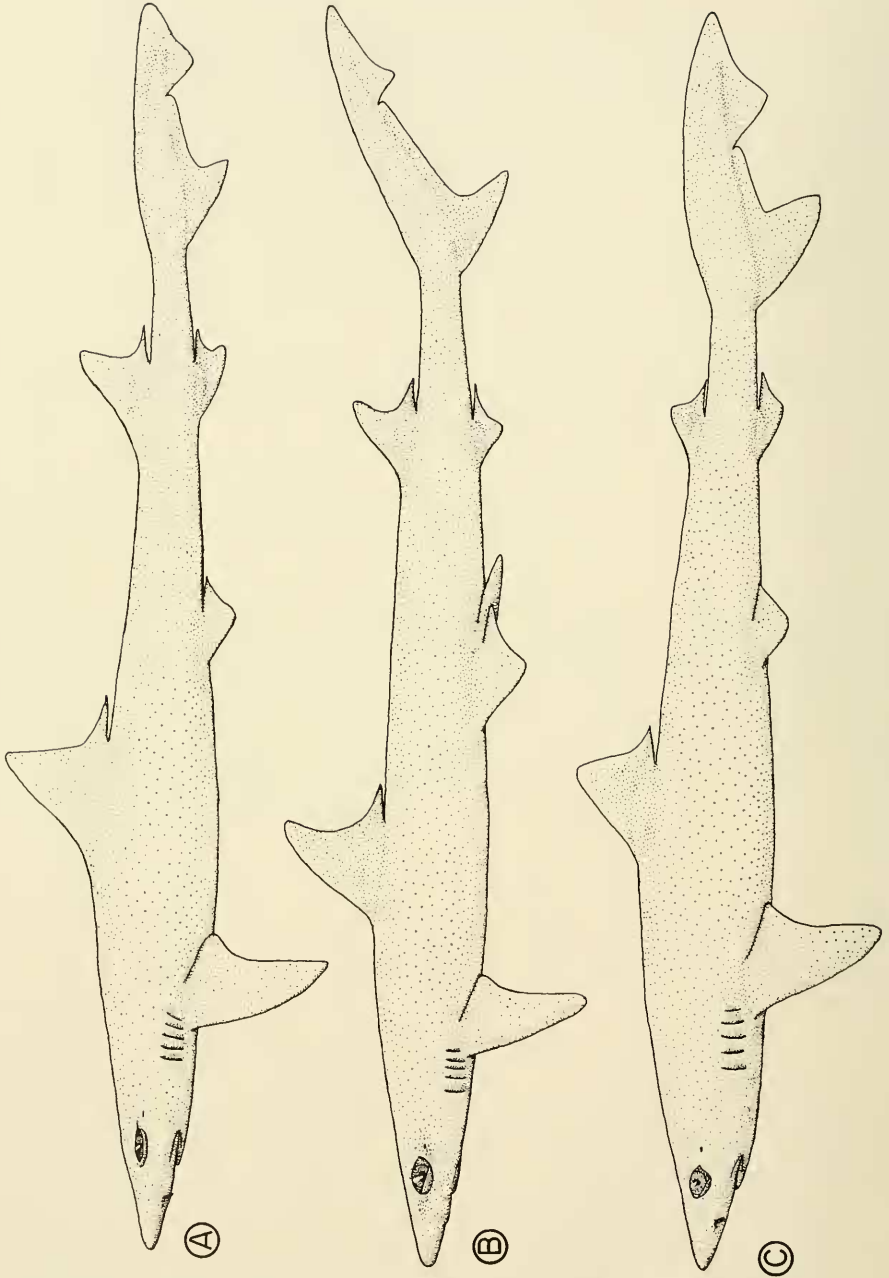


FIGURE 8. Lateral views of carcharhinid sharks. A. *Hemitriakis japonica* (SU-12677). B. *Hypogaleus zanzibariensis* (modified from Smith, 1957b). C. *Galeorhinus zyopterus* (LJVC-0238).

grooves on its teeth (figs. 4B, 4E). *Galeorhinus* and *Hemitriakis* as presently delimited have low roots and strong basal ledges and grooves (figs. 3, 4A, 4D).

Also, Smith did not examine Miyosi's (1939) description of *Galeorhinus hyugaensis*. Comparison of the accounts of *G. hyugaensis* by Miyosi and by Chen (1963) with those of *G. zanzibariensis* by Smith (1957b) and by D'Aubrey (1964) indicates that these species are virtually identical in all important details of morphology (including dentition) and coloration. Indeed, it will be necessary to compare specimens of the two species to determine what differences, if any, exist between them.

Galeorhinus zanzibariensis and *G. hyugaensis* are close to *Galeorhinus* proper and to *Hemitriakis* but are sufficiently different to merit generic status. Hence I propose to raise *Hypogaleus* Smith from subgenus to genus and include in it the two nominal species *H. hyugaensis* (Miyosi, 1939) and *H. zanzibariensis* (Smith, 1957).

The Australian genus *Furgaleus* is included here because its two species, as described and illustrated by Whitley (1943a, 1943b, 1944, 1948), have upper anteroposterior teeth that strongly resemble those of *Hemitriakis*, *Hypogaleus*, and *Galeorhinus*. *Furgaleus* is closest to *Hemitriakis* but is easily distinguished.

The following is a synopsis of *Galeorhinus* and allied genera (including *Hemitriakis*).

1a. Postlateral cusplets absent from anteroposterior teeth in upper jaw. Upper medial teeth without cusplets. First dorsal fin far forward, with origin over anterior half of pectoral base. Caudal fin without ventral lobe in adults "*Galeorhinus*" *omanensis*.

1b. Postlateral cusplets present on upper anteroposterior teeth. Upper medials with both premedial and postlateral cusplets. First dorsal origin posterior to pectoral base insertion. Caudal with moderate to strong ventral lobe in adults 2.

2a(1b.). Nostrils larger and closer together, their widths about twice in internarial width. Nostrils equidistant between snout tip and mouth. Anterior nasal flap formed into a long, slender barbel. Dignathic heterodonty strong, with upper anteroposteriors having oblique primary cusps and postlateral cusplets while lowers have erect primary cusps and no cusplets *Furgaleus*.

2b(1b.). Nostrils smaller and farther apart, their width $2\frac{1}{2}$ times in internarial width or more. Nostrils much closer to mouth than to snout tip. Anterior nasal flap not produced into a barbel. Dignathic heterodonty weak; upper and lower anteroposteriors with oblique primary cusps and postlateral cusplets 3.

3a(2b.). Eyes high on sides of head, above level of nostrils by a space equal to or greater than eye height. Eyes over twice as long as high. NLE external in adults and subadults, with horizontal edge. Anterior nasal flap moderately large, expanded as a rounded lobe. Posterior most anteroposterior teeth elongate, carinate. Interdorsal ridge present. Adult and subadult denticles with crowns much longer than wide and with lateral cusps and ridges weak. Caudal with short ventral lobe in adults and subadults (fig. 8A) *Hemitriakis*.

3b(2b.). Eyes lower on sides of head, above level of nostrils by a space less than eye height. Eyes twice as long as high or less. NLE internal in adults and subadults, with diagonal edge. Anterior nasal flap reduced, expanded as a minute, pointed lobe. Posterior most

anteroposterior teeth not elongate, carinate. Interdorsal ridge absent. Denticles of adults and subadults with crowns nearly as long as wide and with strong lateral cusps and ridges. Caudal with long ventral lobe in adults and subadults 4.

4a(3b.). Head very short, about $\frac{1}{6}$ of total length in adults (fig. 8B). Subocular ridge strong; in dorsal view eyes separated from horizontal head rim by a moderately wide space. Transverse notch absent from tooth roots (fig. 4B). First dorsal as large or larger than pectoral. Second dorsal about $\frac{2}{3}$ as high as first dorsal and about twice as high as anal. Terminal sector of caudal about 2.6 in dorsal caudal margin. Upper postventral margin nearly $\frac{1}{2}$ as long as dorsal caudal margin *Hypogaleus*.

4b(3b.). Head longer, over $\frac{1}{2}$ of total length in adults (fig. 8C). Subocular ridge obsolete; in dorsal view ventral eye margins contact horizontal head rim. Transverse notch present on tooth roots (fig. 4A). First dorsal much smaller than pectoral. Second dorsal less than half as high as first one and subequal to the anal in height. Terminal sector of caudal about 2.0 in dorsal caudal margin. Upper postventral margin only about $\frac{1}{4}$ as long as dorsal caudal margin. *Galeorhinus*.

LEPTOCHARIAS AND *SCYLLIOGALEUS*. Two aberrant, monotypic African genera, *Leptocharias* and *Scylliogaleus*, differ greatly from *Hemitriakis*. While *Scylliogaleus* is apparently closest to typical *Mustelus* species, the taxonomic position of *Leptocharias* is quite isolated in the Carcharhinidae.

Leptocharias, *Hemitriakis*, and *Scylliogaleus* are compared in the following synopsis. Additional data on *Scylliogaleus* is from Boulenger (1902) and Smith (1957c).

1a. Eyes low on sides of head, above level of nostrils by less than eye height. Subocular ridge obsolete; ventral margin of eyes touching horizontal head rim in dorsal view. Eyes less than twice as long as high, with a slant-edged, internal NLE (fig. 2D). Spiracles minute, porelike, less than $\frac{1}{10}$ of eye length. Anterior nasal flap expanded as a pointed barbel. Gynandric heterodontia strong, expressed by presence of about 4 tooth rows of hypertrophied "anterior" in both jaws on either side of weakly differentiated medials in adult males but not females. Teeth other than anterior with slender, erect primary cusps and both premedial and postlateral cusplets, not bladlike or molariform. Vertebrae very numerous, 198-213 total centra (9 examples; data for 2 from Springer and Garrick, 1964). Spiral intestinal valve with about 16 turns. Supraorbital crest absent from cranium, with isolated preorbital and postorbital processes only *Leptocharias*.

1b. Eyes higher, above level of nostrils by an eye height or more. Subocular ridge strong; eyes separated from horizontal head rim by a wide space. Eyes over twice as long as high, with horizontal-edged and external NLE (fig. 7A). Spiracles larger, $\frac{1}{3}$ to $\frac{1}{2}$ of eye length. Anterior nasal flap not formed into a barbel. Gynandric heterodonty not apparent. Teeth either molariform or bladlike, without premedial cusplets (except on medials of *Hemitriakis*). Vertebrae fewer, 143-161 total centra (10 examples). Spiral valve with 6 to 8 turns. Supraorbital crest present on cranium 2.

2a(1b.). Snout bluntly rounded, semicircular in shape. Anterior nasal flaps greatly enlarged as broad triangular lobes extending posteriorly to overlap mouth. Nostrils very large and separated by a distance much shorter than a nostril width. Deep nasoral grooves present. Teeth with crowns flattened and rounded to form a crushing pavement as in typical *Mustelus* species. Teeth not differentiated into medials and anteroposteriors. Tooth rows 60-72 in each jaw; 9-10 series functional in upper jaw, 16-17 in lower (Smith, 1957c).

Pelvis large, anterior margin lengths $\frac{1}{2}$ or more of pectoral anterior margin lengths. Free rear tip of first dorsal over or posterior to pelvic origins *Scylliogaleus*.

2b(1b.). Snout narrower, parabolic in shape. Anterior nasal flaps small truncate lobes, terminating far anterior to mouth. Nostrils smaller, further apart, their widths about $2\frac{1}{2}$ times in internarial width. Nasoral grooves absent. Teeth differentiated into medials and anteroposteriors, not forming a pavement. Anteroposteriors sharp-edged, bladelike teeth, with oblique primary cusps and postlateral cusplets; medials are not bladelike and have premedial cusplets also. Tooth rows fewer, 18(?)–39/27–34; only 1 to 5 series functional along jaw edges. Pelvis smaller, their anterior margins less than $\frac{1}{2}$ length of anterior pectoral margins. Free rear tip of first dorsal anterior to pelvic origins *Hemitriakis*.

TRIAKIS AND ASSOCIATED GENERA. Included here are those species placed by Bigelow and Schroeder (1948) and by Kato (1968) in the genera *Triakis*, *Mustelus*, *Eridacnis*, and *Calliscyllium*.

The systematics of *Triakis* and its relatives is unsatisfactory at present. This is in part due to the interpretations of *Triakis* by Garman (1913), Fowler (1929, 1941), Bigelow and Schroeder (1944, 1948), Garrick (1954), Kato (1968), and Springer (1968), which included several scyliorhinid-like species in this genus that are clearly not congeneric with typical *Triakis* species (as *T. scyllia* and *T. semifasciata*). Also, the separation of *Triakis* from *Mustelus* on differences in tooth crown morphology seems untenable, as there are many dentitionally intermediate species between "typical" extremes of these genera. Bigelow and Schroeder (1940) and Kato (1968) have discussed the latter problem in detail, but left the two genera separate.

Smith (1957a) proposed a solution to the *Triakis* heterogeneity problem. He removed *Calliscyllium venustum* Tanaka from *Triakis* and reinstated *Calliscyllium* Tanaka as a monotypic genus for it. Also, he proposed the genus *Neotriakis* for his *N. simuans* and for *Triakis barbowi* Bigelow and Schroeder. Finally, he transferred *Triakis henlei* (Gill) to *Mustelus*.

Smith's separation of *Calliscyllium* and *Neotriakis* from *Triakis* is undoubtedly correct, as species included in these scyliorhiniform genera exhibit many differences from typical *Triakis*. Unfortunately, Smith retained two anomalous species, *Triakis attenuata* Garrick and *Hemitriakis leucoperiptera* Herre, in the genus *Triakis*. *Triakis attenuata* is closer to *Calliscyllium* and *Neotriakis* in the sense of Smith than to *Triakis* proper, and its presence in *Triakis* makes separation of that genus from *Neotriakis* especially difficult with the limited and ambiguous generic characters utilized by Smith to define these genera. Finally, placement of *Triakis henlei* in *Mustelus* further undermines the classical tooth crown differences purported to separate *Triakis* from *Mustelus*; however, *T. henlei* is closer to typical forms of *Mustelus* than to those typical of *Triakis* in many respects. Smith was evidently unaware of the *Triakis*-*Mustelus* continuity problem, as he later (1957c) gave *Mustelus* familial separation from *Triakis* in his family Scylliogaleidae (along with *Scylliogaleus*).

A tentative reclassification of *Triakis* and associated genera is presented here, subdividing these taxa into two groups: 1. Typical forms of *Triakis*, intergrading species, and typical *Mustelus* forms. 2. Scyliorhiniform triakoids, including as subgroups: A. Genus *Proscyllium*; B. Genus *Eridacnis*; C. *Triakis fehlmanni*; D. *T. attenuata*.

Triakis, *Mustelus*, and intermediates (or *Triakis-Mustelus*) are closer to *Hemistriakis* than are other carcharhinids. *Triakis-Mustelus* includes *Triakis scyllia*, *T. semifasciata*, *T. maculata*, *T. acutipinna*, *Mustelus henlei*, and the various other *Mustelus* species.

Typical species of *Triakis*, with strongly cuspidate teeth (*T. scyllia*, *T. semifasciata*), form one extreme of a dentitional continuum with molariform-toothed *Mustelus* species at the other extreme. The continuum is filled by a host of dentitionally intermediate forms, as *T. maculata*, *T. acutipinna*, *Mustelus nigropunctatus*, *M. henlei*, *M. dorsalis*, *M. megalopterus*, *M. natalensis*, and *M. higmani*, that exhibit various stages of cusp and cusplet reduction on tooth crowns. Also, examination of small (150–450 mm. total length range) specimens of typical *Mustelus* species, as *M. canis*, *M. californicus*, *M. manazo*, *M. mustelus*, *M. lunulatus*, and *M. griseus*, indicates that cusps are often well developed on the teeth of small individuals and that cusp obsolescence in larger examples probably results from ontogenic heterodonty.

Although condition of tooth cusps has been the only character regularly utilized in separating *Triakis* from *Mustelus*, extremes of the former genus differ from typical members of the latter by a number of additional characters. These include: 1. Absence of peg on inner face of crown and root. 2. Lesser number of tooth rows. 3. Lesser number of tooth series. 4. Absence of a tooth pavement. 5. Bluntly rounded, short snout (versus long, pointed or paraboloid snout in *Mustelus*). 6. Very short, arcuate mouth (versus longer, more angular mouth in many *Mustelus* species). 7. Reproduction ovoviviparous (viviparous in at least some *Mustelus*, including *M. henlei*). In addition, there are about a dozen cranial differences between *Triakis semifasciata* and 3 species of *Mustelus* (*M. henlei*, *M. californicus*, and *M. lunulatus*, which are virtually identical cranially). The brain, cranial nerves, and sense organs of *T. semifasciata* also differ in several respects from those of *M. henlei*.

The tooth peg is found in many *Mustelus* species (including *M. henlei*), but not in *Triakis maculata*, *T. scyllia*, or *T. semifasciata*. Its condition is not confirmed for all species of *Triakis-Mustelus* and cannot be used to separate the two genera at present. Tooth row and series counts apparently vary along a continuum as in crown morphology, with an added complication that in at least some *Mustelus* (if not all forms) the tooth row and series counts increase with size increase. Tooth pavementization, snout shape, and mouth morphology evidently show a similar variation spectrum. Data on cranial, neural, and repro-



ductive characters is not available for many to most *Triakis-Mustelus* species, making it impossible to judge their utility in separating the two genera.

External morphology suggests that *Triakis* is not separable from *Mustelus*, but merging the two genera here would be premature with incomplete knowledge of promising anatomical characters. However, *Triakis-Mustelus* is treated as a single unit here for comparison with *Hemitriakis*.

The scyliorhiniform triakoids include species formerly placed in the genera *Proscyllium*, *Calliscyllium*, *Eridacnis*, *Neotriakis*, and *Triakis*. They are divisible into four subgroups, two of which are provisionally ranked as genera.

The first genus, *Proscyllium*, is a structural link between the Carcharhinidae and Scyliorhinidae but is placed in the former family because of its anteriorly positioned first dorsal fin.

The systematic treatment of *Proscyllium* and its synonym, *Calliscyllium*, by various writers has been highly variable and extremely confusing. Hilgendorf (1904) proposed *Proscyllium* as a subgenus of *Scyllium* Cuvier (= *Scylliorhinus* Blainville), with a single new species, *S. (Proscyllium) habereri*, from Formosa. Later Tanaka (1912) described a new genus and species, *Calliscyllium venustum*, from Japan. Tanaka did not mention Hilgendorf's very similar species in his account. Although Tanaka considered *Calliscyllium* a scyliorhinid, Garman (1913) placed it in his family Galeorhinidae (= Triakidae) and synonymized it with *Triakis*. Garman also placed *Scyllium (Proscyllium) habereri* in the Catulidae (= Scyliorhinidae) and raised the rank of *Proscyllium* to genus. Schmidt (1930) described and illustrated a Japanese specimen of *Proscyllium habereri*. His account is of special interest as he compared his specimen with measurements and photographs of the holotype of Hilgendorf's species and found no significant differences between the two specimens. Schmidt's account of *Proscyllium habereri* closely matches Tanaka's description of *Calliscyllium venustum*, but for unknown reasons Schmidt did not refer to Tanaka's account or to his own (1928) description of an Okinawan specimen of *Calliscyllium venustum*. White (1937) recognized both *Calliscyllium venustum* and *Proscyllium habereri* as scyliorhinids in a broad sense but placed the former in her family Halaeluridae and the latter in her family Catulidae. Fowler (1929, 1941) followed Garman in placing *Proscyllium* in Scyliorhinidae and placed *Triakis venusta* (Tanaka) in the subfamily Triakiinae of the family Eulamiidae or Galeorhinidae (= Carcharhinidae). Bigelow and Schroeder (1948) placed *Proscyllium habereri* in the family Triakidae, but did not discuss its generic status in that family. These writers followed Garman's synonymy of *Calliscyllium* with *Triakis*. Garrick (1954) discussed *Triakis venusta*, but not *Proscyllium habereri*. Smith (1957a) recognized *Calliscyllium* as distinct from *Triakis*, but also overlooked *Proscyllium habereri*. Lindberg and Legeza (1959) synonymized *Proscyllium* with *Triakis*, but considered

Triakis habereri distinct from *T. venusta*. Chen (1963) placed both *Proscyllium habereri* and *Triakis venusta* in the family Triakidae, but separated *Proscyllium* from *Triakis* by supposed absence of the NLE in the former genus. Finally, Kato (1968) removed *Calliscyllium* from synonymy of *Triakis* on reproductive differences, but did not mention *Proscyllium*.

Comparison of accounts of *Proscyllium habereri* and *Calliscyllium venustum* with each other and with specimens indicates that Lindberg and Legeza were correct in regarding these species as congeneric. However, “*venustum*” and “*habereri*” are not congeneric with typical species of *Triakis* and are placed here in the genus *Proscyllium*. *Calliscyllium* is therefore a junior synonym of *Proscyllium*. The two species *P. venustum* and *P. habereri* are possibly synonyms also, as the small differences between them listed by Lindberg and Legeza (1959) may be of only variational and allometric significance.

The genus *Eridacnis* includes a few species of deepwater sharklets allied to *Proscyllium* but sufficiently different to merit generic status.

Eridacnis was established by Smith (1913) for *E. radcliffei*, a new shark from the Philippine Islands. *Eridacnis* was supposed to differ from *Triakis* Müller and Henle by lacking labial furrows, but, as Kato (1968) pointed out, the holotype of *E. radcliffei* has vestigial labial furrows presumably overlooked by Smith. Bigelow and Schroeder (1944) described as *Triakis barbouri* a similar but specifically distinct shark from Cuba, but did not compare it with *Eridacnis radcliffei*. Misra (1950) described a third form, *Proscyllium alcocki*, from the Andaman Sea. Data from Misra's account indicates that “*alcocki*” does not belong in *Proscyllium* as here defined but falls in *Eridacnis* instead. The species “*alcocki*” closely resembles *E. radcliffei* and therefore it is quite possible that these two names are synonymous (Norman, 1939, reported *E. radcliffei* from the Gulf of Aden, which is west of the type localities of both *E. radcliffei* and “*alcocki*”). Smith (1957a) described a new genus, *Neotriakis*, for his new South African species *N. sinuans*. Smith included *Triakis barbouri* in *Neotriakis* but overlooked *Proscyllium alcocki* and did not compare *Neotriakis* species with the closely similar *Eridacnis radcliffei*. Kato (1968) considered the characters used to separate *Neotriakis* and *Eridacnis* from *Triakis* to be untenable, and synonymized the three genera. However, Kato regarded the species “*radcliffei*,” “*barbouri*,” and “*sinuans*” as closely related to each other within the genus *Triakis*. Kato's synonymy was adopted unchanged by Springer (1968).

The genus *Eridacnis* is revived here for the species *E. radcliffei*, *E. alcocki*, *E. barbouri*, and *E. sinuans*, with *Neotriakis* considered as a junior synonym.

Triakis fehlmanni, a small shark recently described by Springer (1968) from Somalia, forms a third group closely similar to *Proscyllium* and *Eridacnis* in many details. Its vertebral calcification pattern and relatively short broad caudal are as in *Proscyllium*, but its vertebral count, vertebral group ratios, short

body cavity, nostril spacing, pectoral fin position, first dorsal size, and anal base size fit *Eridacnis*. The blotched and spotted color pattern, extremely short pre-caudal tail (distance from cloaca to lower caudal origin about twice in distance from snout tip to cloaca), broad head, and stout body distinguish "*fehlmanni*" from both *Proscyllium* and *Eridacnis*. Mode of reproduction and clasper morphology are unknown for the species. *Triakis fehlmanni* seems closer to *Eridacnis* than *Proscyllium* but may require subgeneric or generic separation from typical *Eridacnis* species. It does not belong to *Triakis-Mustelus* as here limited and cannot be confused with *Hemitriakis*. Generic placement of "*fehlmanni*" is problematical at present; therefore the species must be left as a tentative and possibly dubious appendage to *Eridacnis*.

The New Zealand *Triakis attenuata*, as described by Garrick (1954), agrees with *Proscyllium*, *Eridacnis*, and *T. fehlmanni* in its NLE type, detailed tooth morphology, eye position, and large second dorsal, but differs from these forms in its elongate snout, narrower and more widely spaced nostrils, longer labial furrows, more numerous tooth rows, more anterior position of first dorsal fin, origin of second dorsal anterior to anal origin, exceptionally small anal fin with base only half length of second dorsal base, weak ventral caudal lobe, and larger size. Unfortunately nothing is known of its cranium, pectoral fin skeleton, vertebral calcification pattern, vertebral counts, vertebral group ratios, clasper morphology, and buccal cavity. *Triakis attenuata* presumably forms a tentative fourth group of scyliorhiniform triakoids allied to, but distinct from, *Proscyllium-Eridacnis-T. fehlmanni*. The species is remote from *Hemitriakis* and is sufficiently different from *Triakis-Mustelus* to be excluded from that group. Separate generic status may be required for *T. attenuata*, but insufficient data on the species prohibits a decision on the matter for now.

The following generic synopsis compares *Hemitriakis* to *Triakis-Mustelus*, *Proscyllium*, and *Eridacnis* (excluding *T. fehlmanni*).

1a. NLE rudimentary in adults (fig. 2A.). Labial furrows vestigial, confined to corners of mouth. All teeth with erect cusps and usually cusplets also (some species have teeth near symphysis lacking cusplets). Posterior teeth polycuspidate, comblike in shape (fig. 4C). Gradient monognathic heterodonty present, in which premedial cusplets increase in number from symphysis to rictus and displace primary cusp from central position on crown foot to a postlateral location. Cusps and cusplets do not become obsolete with age. First dorsal fin with midpoint of its base closer to pelvic origins than to pectoral insertions. Second dorsal origin over or posterior to anal origin. Pectoral fin skeleton as in scyliorhinids, with distal radials much shorter than proximal ones. Vertebral centra of thoracic region in adults with peripheral calcifications of the intermedialia only, not developed into strong lateral and vertical wedges between halves of calcified primary double cone (figs. 5A, 5B.). Diagonal calcified lamellae of double cone, when present, in form of rounded lobe opposite each basidorsal and basiventral. Large papillae present on dorsal and ventral surfaces of buccal cavity and pharynx posterior to teeth, forming dermal gill rakers along internal branchial apertures 2.

1b. NLE external, transitional, or internal in adults. Labial furrows well developed,

extending far onto jaws. Teeth either cusplless or with cusps that range from erect to strongly oblique and often showing monognathic heterodonty in increasing obliqueness toward ends of dental band. Posterior teeth carinate, molariform, or weakly monocuspidate, not comblike (fig. 4F.). Increase of premedial cusplets and displacement of primary cusp postlaterally not apparent in species with cuspidate teeth, but instead cusps and cusplets tend to become less prominent postlaterally and may be completely absent on posteriormost teeth. Many species (not including *Hemitriakis*) tend to reduce or lose cusplets or even cusps with age. First dorsal fin with base midpoint equidistant between pectoral insertions and pelvic origins or closer to pectoral insertions. Second dorsal origin well anterior to anal origin. Pectoral fin skeleton with distal radials equal in length to, or longer than, proximal ones. Vertebral centra of thoracic region of adults and subadults with intermedialia extending as strong lateral and vertical wedge-like calcifications between halves of calcified primary double cone (figs. 5C, 5D.). Diagonal calcified lamellae well developed, extending as thin plates into the basidorsals and basiventrals. Papillae absent from buccal cavity, pharynx, and internal branchial apertures

2a(1a.). Nostrils very close together, internarial width only $\frac{1}{2}$ nostril width. Distance from hind edge of anterior nasal flaps to mouth only about $\frac{1}{6}$ of nostril width. Head length from snout tip to 5th gill opening shorter than body length from pectoral insertion to pelvic origin. First dorsal length from origin to free rear tip less than $\frac{1}{2}$ length of interdorsal space. Anal base length only $\frac{1}{2}$ of distance between anal insertion and lower caudal origin. Caudal short, less than $\frac{1}{5}$ of total length. Greatest height of caudal about $\frac{1}{4}$ of upper caudal margin. Vertebrae more numerous, total count 146-168 (6 examples). DP/MP ratios 1.58-1.82; DC/MP 1.08-1.28. Diagonal calcified lamellae of trunk centra present as four rounded lobes extending slightly into areas of basidorsals and basiventrals (fig. 5B.). Claspers of adult males with a row of recurved clasper hooks along external flap of hypopyle. Color pattern of scylliorhinid-like spots and stripes present. Reproduction oviparous *Proscyllium*.

2b(1b.). Nostrils farther apart, internarial width about equal to nostril width. Distance from hind edge of anterior nasal flaps to mouth about $\frac{1}{2}$ of nostril width. Head length longer than body length from pectoral to pelvic. First dorsal length $\frac{3}{5}$ to $\frac{4}{5}$ of interdorsal space. Anal base length subequal to distance between anal insertion and lower caudal origin. Caudal longer, over $\frac{1}{4}$ of total length. Greatest height of caudal less than $\frac{1}{5}$ of upper caudal margin. Vertebrae less numerous, total count 113-135 (26 examples). DP/MP ratios 1.05-1.45; DC/MP 1.29-1.53. Diagonal calcified lamellae not developed in trunk centra (fig. 5A.). Claspers without hooks. Coloration plain or with a few obscure stripes confined to tail. Reproduction ovoviviparous as far as is known *Eridacnis*.

3a(1b.). Nostrils narrow and farther apart; nostril width about $2\frac{1}{2}$ times in internarial width. Teeth larger, basal width of largest lower anteroposteriors about 0.356 to 0.405 percent of total length (*H. japonica*, 4 examples). Teeth differentiated into medials and anteroposteriors. The latter are strongly compressed, bladelike cutting teeth with an oblique primary cusp and a few small postlateral cusplets only. Fewer tooth rows present, ?18-38/24-34. Pelvic fins with anterior margins less than half as long as pectoral anterior margins *Hemitriakis*.

3b(1b.). Nostrils wider, closer together; nostril width 2 times or less in internarial. Teeth smaller, those of species with largest teeth (*Triakis semifasciata*) only 0.172 to 0.262 percent of total length (largest lower teeth, 11 examples) and considerably smaller in other species. Teeth not differentiated into distinct medials and anteroposteriors, but showing regular gradient monognathic heterodonty between rows in symphyssial and parasymphyssial regions. Teeth corresponding to anteroposteriors of *Hemitriakis* either cusplless or having

an erect or oblique median primary cusp and usually both premedial and postlateral cusplets when cusplets are present. Teeth more weakly compressed, not sharp-edged, modified for grasping or crushing. More tooth rows present, 44-80+/33-80+. Pelvic fins larger, with anterior margins over $\frac{1}{2}$ as long as pectoral anterior margins -----
----- *Triakis-Mustelus*.

SUMMARY

The shark *Galeus japonicus* Müller and Henle, long considered a species of *Galeorhinus* Blainville (or one of its synonyms), is placed in the genus *Hemitriakis* Herre, which is removed from the synonymy of *Triakis* Müller and Henle and redefined. *Hemitriakis* contains two described species, *H. japonica* (Müller and Henle) and *H. leucoperiptera* Herre.

The familial position of *Hemitriakis* is discussed and the separation of the families Triakidae and Carcharhinidae is rejected on present evidence. *Hemitriakis* is placed in the expanded family Carcharhinidae.

Other carcharhinid genera are compared with *Hemitriakis* in synoptic keys, and several tentative systematic rearrangements of species in certain genera are presented to facilitate comparison with *Hemitriakis*. The genus *Galeorhinus* is restricted to the nominal species *G. galeus*, *G. australis*, *G. zyopterus*, *G. chilensis*, and *G. vitaminicus*, while a former subgenus, *Hypogaleus* Smith, is accorded generic rank. *Hypogaleus* contains two nominal species, *H. zanzibariensis* (Smith) and *H. hyugaensis* (Miyosi). Consideration of *Galeorhinus omanensis* (Norman) is postponed for another paper.

In addition to *Hemitriakis*, four tentative groups of scyliorhiniform triakoids are removed from *Triakis*. The first is the genus *Proscyllium* Hilgendorf, of which *Calliscyllium* Tanaka is a junior synonym. *Proscyllium* has two nominal species, *P. habereri* (Hilgendorf) and *P. venustum* (Tanaka). The genus *Eridacnis* Smith forms the second group, with *E. radcliffei* Smith, *E. barbouri* (Bigelow and Schroeder), *E. sinuans* (Smith), and the dubious *E. alcocki* (Misra) as its constituent species. The last two groups contain *Triakis fehlmanni* Springer and *T. attenuata* Garrick; these are not given genus-group names because of insufficient evidence on the generic relationships of their species.

The problem of separating the restricted genus *Triakis* from *Mustelus* Linck is discussed, but no solution is seen at present and the two genera are considered as one unit for comparison with *Hemitriakis*.

A terminology for head morphology, nictitating lower eyelid structure, dentition, vertebral groups, and fin morphology is proposed for use with carcharhinids.

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